Placoderm Interrelationships: a new Interpretation, with a short Review of Placoderm Classifications

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Some of the major classifications of placoderms are briefly reviewed, in their relation to phylogenetic ideas about the group, and the more recent hypotheses of placoderm interrelationships are critically evaluated. Using reinterpreted characters (body armour composition, skull-roof bone pattern, tesserae, number of paranuchal plates, endolymphatic duct, position of nasal capsules, cervical joint, claspers, ornamentation and histology of the dermal bone), a new cladogram, based on 50 synapomorphies, is proposed for all placoderm orders except stensioellids and pseudopetalichthyids, which remain too poorly known. Two main divisions are recognized. In the first branch arthrodires, phyllolepids, petalichthyids and ptyctodontids are characterized by their ventral body armour with an anterior median ventral plate. The second branch groups acanthothoracids, antiarchs and rhenanids on two synapomorphies: a premedian plate, and dorsal nasal capsules. Other synapomorphies (tesserae, structure of the shoulder girdle, and of the cervical joint) require the Acanthothoraci to be dismembered into at least two groups linked respectively to the rhenanids (tesserate forms) or to the antiarchs. The position of *Radotina prima* is also discussed. As a main conclusion, arthrodires and antiarchs are no longer considered as sister-groups. Their elongated body armour is seen as a result of convergent adaptation. The various acanthothoracids share synapomorphies with one or other of the two main divisions, and the Acanthothoraci therefore forms a stem-group of imprecise phylogenetic status.

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A SHORT HISTORY OF PLACODERM CLASSIFICATIONS AND THEIR MEANING

M'Coy (1848) created the name Placodermi to distinguish, among the 'ganoids', a family grouping the genera *Asterolepis, Pterichthys, Bothriolepis, Coccosteus* and *Chelyophorus,* and also the ostracoderm agnathan *Psammosteus.* Since then the definition and classification of placoderm fishes have undergone a number of different versions, as summarized by Obruchev (1964, 1967). My purpose here is to consider only those which represent the major steps in our understanding of the placoderm concept.

During the second half of the nineteenth century and up to 1930 the unity of the group had been rejected by a majority of authors, who followed Cope (1889) and Woodward (1891) in linking ptyctodontids generally to holocephalans, antiarchs to ostracoderm agnathans, and the arthrodires (a name created by Woodward in 1891 for the 'Coccosteans' of previous authors) to the dipnoans. However Dean (1899, 1901) and Hussakof (1905, 1906) recommended keeping apart the arthrodires from lungfishes, and created a separate class, the Arthrognathi.

Since then the unity of Placodermi has been gradually restored, first by Stensiö (1925), who allied petalichthyids, ptyctodontids, and rhenanids to the arthrodires, without erecting a new classification. Later, Stensiö (1931), Gross (1931), and Heintz (1932) returned the antiarchs to the group, Heintz including them in the class

Placodermata as a sub-class equivalent to the Arthrodira, which then comprised only the orders Acanthaspida (Dolichothoraci or Arctolepida), and Coccosteida (= coccosteids + pachyosteids).

Among the classifications of the first half of this century, the following, by Gross (1937), was most influential, and formed a basis for a number of works, some fairly recent (e.g. Denison, 1958; Miles, 1967):

Phylum Elasmobranchi
        Class: Placodermi
        1st Group: Antiarchi
        2nd Group: Arthrodira
            Order 1: Euarthrodira
                Suborder: Acanthaspida (= Arctolepida)
                Suborder: Brachythoraci
            Order 2: Phyllolepida
            Order 3: Petalichthyida
            Order 4: Ptyctodontida
        3rd Group: Rhenanida
        4th Group: Stegoselachii

This classification thus included all major groups except the Acanthothoraci (= Palaeacanthaspida), which was defined later by Stensiö (1944). In it, Gross expressed the gradual evolution of the body armour. He assumed that the long armour of antiarch or dolichothoracid type was a primitive state, and the short armour was specialized. This derived from a progressive reduction in length of the flanks of the body armour observed in arthrodires, from the 'Acanthaspida' (Dolichothoraci) of the Early Devonian, to the Late Devonian Pachyosteomorphi. Gross then transposed such a model to the Placodermi as a whole.

Westoll (1945) interpreted the evolution of the group according to similar processes, but proposed a different grouping: the Arthrodira, Petalichthyida (uniting the Macropetalichthyida and Rhenanida), and Antiarcha (sic) were ranked as separate orders in the class Placodermi. If phylogeny is considered to represent the sequence of formation of monophyletic groups, these classifications are not really phyletic. They do not express the assumed relationships between various members of the class Placodermi, but only a gradual morphological transformation series of one character, the body armour.

Stensiö's classifications (1944, 1959, 1963, 1969) were built on the same general principle, but on a different basic assumption. He organized the Placodermi according to their relative degree of fin concentration and the length of the endoskeletal pectoral articulation. Fin evolution was considered to reflect the ontogenetic development of the paired fins in selachians, according to the fin-fold theory of Gegenbaur and Goodrich (1909). An initially long based fin, and a body armour devoid of spinal plate (as in the 'Pachyosteomorph arthrodires'), supposedly gave rise to a highly concentrated fin, as exemplified by the antiarchs. In the last of Stensiö's classifications, the placoderms (named Arthrodira) are distributed in two major groups: Euarthrodira and Antiarchi. The first group includes two super-orders: the 'primitive' Aspinothoracidi, lacking a spinal plate and showing a long-based pectoral fin, and the 'more advanced' Spinothoracidi, possessing a spinal plate, which supposedly developed by fusion of the anterior fin radials, and a 'concentrated' pectoral fin. Stensiö proposed (1969: 153) that the spinothoracid arthrodires 'should have evolved partly from early primitive prearthrodires, and partly from some Aspinothoracidi'. The groups are, in that case, evidently founded on parallelism or convergence.

Under this classification, the subsets may not correspond to natural (monophyletic) groups, and euarthrodire families are kept apart which, in view of their shared specializations, should be grouped together. The morphological basis for this classification is also undermined because some of the so-called Aspinothoracidi possess a spinal plate (Mark-Kurik, 1963; Heintz, 1968). Stensiö (1969: 53) evaded this problem by considering in these cases that it represented a 'pseudo-spinal' plate, not homologous to the true spinal, even if it occupied the same position, with the same basic function of fixing together dorsal and ventral halves of the armour and covering the endoskeletal scapulo-coracoid.

But the major drawback of Stensiö's classification is the confusion caused by using the same terminology as other authors to qualify different taxa. Under the name Arthrodira are grouped all the placoderms of the other authors; the term Placodermata (sic) then designates the set composed of the Arthrodira and the Holocephali, which are supposed to be ptyctodontid descendants (Ørvig, 1962). The name Euarthrodira, also kept by Stensiö, designates all the non-antiarch placoderms of the other authors.

A different attitude was expressed in the classifications of Romer (1966) and Miles (1969). The practical aspect was emphasized, to give an organized list of clearly defined orders, which may or may not be monophyletic. No supra-ordinal groupings were proposed, so there is no real hierarchical classing. Although not expressing any ideas on the interrelationships of the groups of placoderms, such classifications have the advantage of flexibility in permitting the possible affinities between groups to be worked out without remodelling all taxonomic ranks and the associated nomenclature.

However it is still necessary to go beyond such a state of our knowledge, and to build up a phylogenetic hypothesis of relationships which, by initiating new research, can enrich our information on all the placoderm groups. In our present state of knowledge any attempt of that sort cannot claim to be more than a working hypothesis. To remain in the realm of scientific enquiry, in the sense of Popper (1973), the hypothesis must be testable. For this it must meet certain methodological requirements, but most importantly, it must be as explicit and comprehensive as possible to permit corroboration or refutation.

PLACODERM INTERRELATIONSHIPS: SOME RECENT HYPOTHESES

Although different, the hypotheses of placoderm interrelationships proposed by Denison (1975, 1978) on the one hand, and by Miles (1973), Miles and Young (1977), and Young (1980) on the other, adhere to such principles. These schemes are my initial working hypotheses to grapple with the problems of placoderm interrelationships. Both schemes are based on characters of the body armour and associated structures like the dermal cervical joint. Denison takes also into account other criteria like the pattern of dermal bones in the skull, and the nature of the superficial skeletal tissue of the dermal bone.

The proposals of these authors will be discussed here using characters deduced from the study of the skull-roof and endocranium, and a revision of the supposed homologous structures in the body armour. However, to avoid doubtful interpretations of material rather badly known and hard to analyse, I will not include the Stensioellidae and the Pseudopetalichthyidae. These occupy an important position in Denison's phylogeny, as models for the primitive condition of many characters. I will also initially assume that the various placoderm orders (arthrodires, antiarchs, phyllolepids, rhenanids, acanthothoracids, ptyctodontids, and petalichthyids) are monophyletic groups in the sense of Hennig (1966).

Denison's phylogeny scheme (Fig. 1) differs from that of Miles and Young (1977) both in its initial assumptions, and in the methodology used to reconstruct phylogenies.

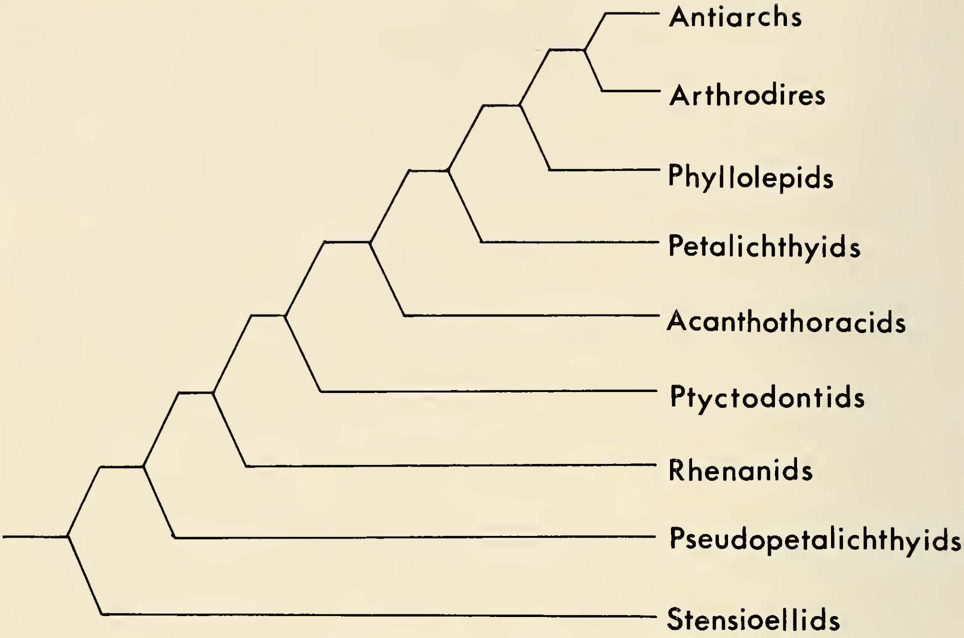

Fig. 1. Denison's phylogeny of placoderms (after Denison, 1978: fig. 10).

Miles and Young adopt a strictly cladistic attitude, but Denison admits, as a methodological principle, the search for ancestor-descendant relationships. Thus, he classifies monophyletic groups with others which are not, causing confusion in the composition, understanding, and definition of higher ranked groups. This applies mainly to the arthrodires, and actinolepid arthrodires are a 'grade' group, from which the other arthrodires, phyllolepids, and the antiarchs are thought to arise.

Another initial assumption is that Denison apparently shares Schaeffer's opinion (1975) that placoderms are the sister-group of all other gnathostomes. He assumes that a short body armour is the primitive condition of placoderms, and that distinctive specializations in the various groups can be used as the foundations of a phylogenetic classification. He proposes a number of primitive characters based on the morphology of stensioellids, pseudopetalichthyids, and ptyctodontids, but he also refers to acanthothoracids and rhenanids. Among the 18 primitive characters listed by Denison (1975), the following 15 can be discussed as relevant to this study:

1) The ventral shoulder girdle consists of a single pair of plates homologous either to the interolaterals or the anterior ventrolaterals of the Arthrodira; between them, a median plate has been identified only in Ptyctodontida.

2) The lateral shoulder girdle consists only of anterior laterals and anterior dorsolateral plates, except in some Acanthothoraci where posterolaterals and posterior dorsolaterals are also present.

3) The spinal plates are absent, or small and doubtfully distinct, except in acanthothoracids and ptyctodontids.

4) A medial dorsal is probably absent in stensioellids and pseudopetalichthyids.

5) Pectoral fins are narrow-based, even in rhenanids where the fins are much expanded distally.

6) There is no exoskeletal cervical joint, except in ptyctodontids where it is developed differently from arthrodires and antiarchs.

7) The anterior vertebrae are fused to form a synarcual which articulates with the occipital region of the neurocranium (not known in Acanthothoraci).

8) The neurocranium is long and slender with a long occipital region, except in ptyctodontids where it must have been short.

9) The dermal cranial roof bone pattern may be variable and unstable with relationships between bones and sensory canals not firmly established, except in ptyctodontids.

10) Dermal cranial roof bones may be small, and part of the roof may be covered with thin, superficial tesserae in acanthothoracids and rhenanids; much of the skull in stensioellids is covered with denticles or tesserae; the central part of the cranial roof of pseudopetalichthyids is covered with small dermal bones, but there may have been denticles or tesserae elsewhere. Denticles and tesserae are unknown in ptyctodontids, but may have covered the snout and cheek where dermal bones are largely absent.

11) The jaws, where known, are more or less transverse and lack large dermal elements, except in ptyctodontids.

12) Gill covers (submarginals) may be present, though their dermal bones are small in ptyctodontids.

13) The orbits are small and lateral in stensioellids and most acanthothoracids, large and dorsolateral in ptyctodontids, and dorsal in pseudopetalichthyids, rhenanids, and one late genus of acanthothoracid; the last condition is surely specialized.

14) The nostrils are known only in rhenanids and acanthothoracids where they are usually dorsal, a condition that is surely specialized. In stensioellids, pseudopetalichthyids and primitive acanthothoracids, they are presumed to be anterior or anteroventral; there are no clues of their position in ptyctodontids.

15) Pelvic fins are long-based and semicircular in rhenanids, stensioellids and pseudopetalichthyids; they are specialized by the development of claspers in male ptyctodontids.

On eight of these charactlers (1-4, 8-10, 12), of which they temporarily accepted the validity, Miles and Young (1977: 128) listed nine unparsimonious consequences of Denison's phylogeny. However some of these criticisms follow from a particular interpretation by Miles and Young of Denison's scheme. For example they claim that the loss of the dermal neck-joint in phyllolepids involves a reversal in evolution, but Denison (1975) regarded phyllolepids as more closely related to actinolepids than to the other arthrodires and the antiarchs, and the loss of the neck-joint was therefore not implied. The anterior dorsolateral plate in *Phyllolepis* demonstrates the presence of a sliding dermal neck-joint very similar to that of actinolepid arthrodires (see Stensiö, 1936: pl. 14, fig. 2; Young, 1980: 69).

Miles and Young's (1977) alternative scheme (Fig. 2), is mainly built on features of the body armour. From the distribution of its component bones among the various groups of placoderms, they suggest a hypothetical ancestral morphotype of the armour made up of the following plates: a single median dorsal, paired anterior dorsolaterals, posterior dorsolaterals, anterior laterals, interolaterals, anterior ventrolaterals, and an anterior median ventral. This morphotype also assumes certain homology conventions and postulates which will be discussed later.

Two other characters used are the presence or absence of tesserae, and the number of paranuchal plates (one versus two). The potential phylogenetic importance of these characters had been suggested earlier by Westoll (1967). Miles and Young attempted to elucidate their phylogenetic meaning by analysing the alternative hypothesis, but were unable to select a preferred solution using a parsimony criterion. They concluded

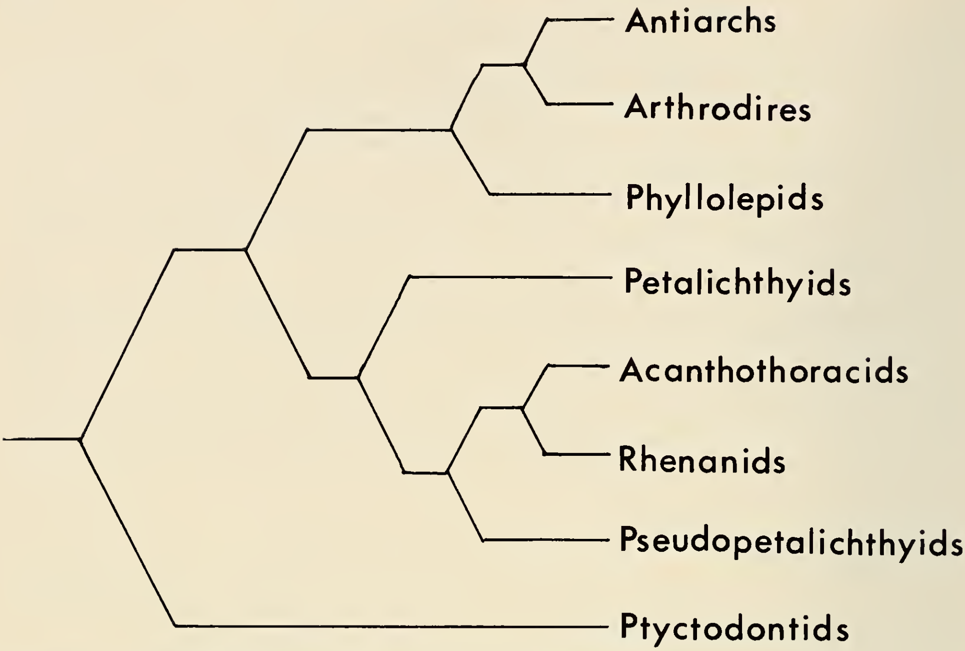

Fig. 2. Miles and Young's phylogeny of placoderms (after Miles and Young, 1977: fig. 5).

that presence of tesserae does not define any important group, because within a supposed monophyletic group (the Acanthothoraci), some members have tesserae and some do not. However they proposed the presence of two paranuchal plates as a synapomorphy uniting petalichthyids, acanthothoracids, rhenanids, and pseudopetalichthyids, but were unable to present strong supporting arguments. In their own words, they admit this character as a valid synapomorphy 'simply on the ground that trial and error has shown it to be the more useful hypothesis for (their) work' (Miles and Young, 1977: 133). In other words, it does not contradict their conclusions based on their trunk armour analysis, and thus might be seen as an 'a priori' statement.

On the other hand, there is no unequivocal evidence of two paranuchal plates in rhenanids (gemuendinids of Miles and Young, 1977), in spite of Westoll's account (1967: fig. 3). In known Acanthothoraci, the homologies of the supposed paranuchal plates are not easily established, and the plate interpreted as a medial paranuchal by Ørvig (1975) in *Romundina* is interpreted as a posterior central by Denison (1978) and Young (1980).

In their final diagram, Miles and Young group the non-ptyctodontid placoderms in two distinct lineages. Arthrodires (Fig. 3**A**, **B**) and antiarchs (Fig. 3**C**, **D**) are united on the presence of posterior ventrolateral, posterior median ventral and posterolateral plates; in other words, they possesss a long body armour. The phyllolepids (Fig. 5**B**) are the only other placoderms supposed to possess a true posterior ventrolateral; this is interpreted as a synapomorphy linking them to the arthrodires and antiarchs. The second lineage groups the petalichthyids (Fig. 7**D**), acanthothoracids (Figs 8, 9), rhenanids (Fig. 7**I**) and pseudopetalichthyids. The supposed uniquely derived shared characters of these groups are two pairs of paranuchals, and a long occipital region of

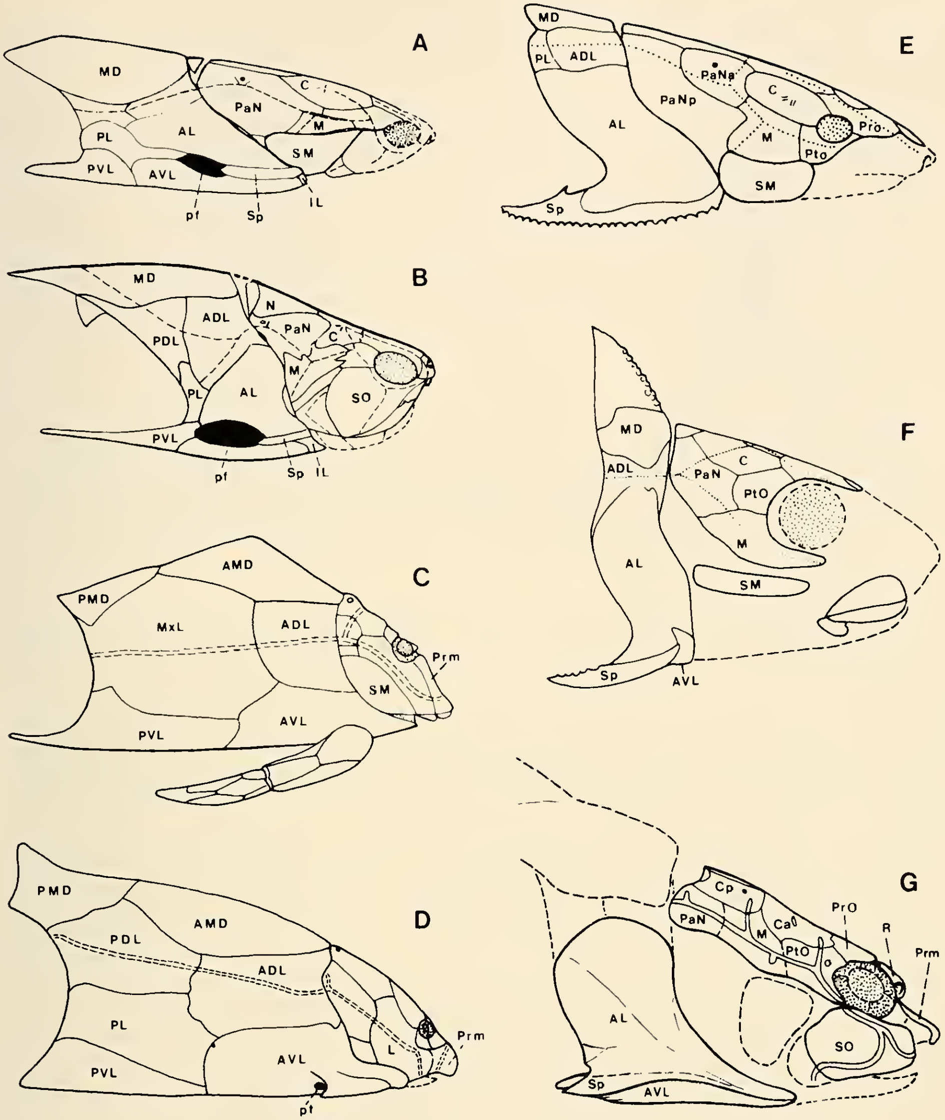

Fig. 3. Lateral view of the dermal armour in representatives of the various placoderm groups. **A**, actinolepid arthrodire: *Sigaspis lepidophora,* from Goujet (1973). × 0.6. **B**, brachythoracid arthrodire: *Coccosteus cuspidatus,* from Miles and Westoll (1968). × 0.4. **C**, asterolepid antiarch: *Pterichthyodes milleri*, from Traquair (1914). × 0.4. **D**, yunnanolepid antiarch: *Yunnanolepis parvus,* from Zhang (1978). × 2.4. **E**, petalichthyid: *Lunaspis heroldi,* simplified from Stensiö (1963). × 0.5. **F**, ptyctodontid, *Rhamphodopsis threiplandi,* from Miles (1967). × 2.4. **G**, acanthothoracid: *Romundina stellina*, slightly modified from Ørvig (1975). × 2.3.

the skull. Acanthothoracids and rhenanids are also assessed as sister-groups on one common specialization: the dorsal position of the nasal apertures (Fig. 10**A**, **B**, **D**). A premedian plate may be linked to this character, but Miles and Young note that this plate had not been clearly demonstrated in rhenanids. They conclude that the premedian plate in acanthothoracids and antiarchs has originated independently, but this contradicts the rule of bone regression they advocate as a low level evolutionary law. According to this rule, they claim to have been more ready to accept the multiple loss of bones than their multiple origin.

The dorsal position of the nasal apertures back from the rostral margin is in my opinion a major feature which influenced the whole development of the front part of the endocranium and the morphology of the brain cavity. This feature appears underestimated by Miles and Young, and if it could be shown that the resemblances of the body armour are less important than they propose, the nasal position would suggest a closer relationship between antiarchs and acanthothoracids.

To place ptyctodontids within their phylogenetic scheme Miles and Young use a primary sexual character: the pelvic and prepelvic claspers. This appeal to structures otherwise known only in elasmobranch fishes implies that they consider placoderms to be elasmobranchiomorphs.

Reanalysis of Phylogenetically Important Characters

Miles and Young's hypothesis appears more parsimonious than Denison's, but it is built on preliminary choices and assumptions about the significance of paranuchal plates and the body armour composition which call for discussion. This discussion will be the source of different ideas from which a new hypothesis of placoderm interrelationships will be proposed.

THE BODY ARMOUR (Figs 3, 4, 5)

The primitive composition of the body armour proposed by Miles and Young presupposes several hypotheses about the homology of various plates. Thus they suggest the term 'anterior ventrolateral', and not 'interolateral', for the single paired plate in the anterior ventral position of ptyctodontids (Fig. 5**C**) and rhenanids (Fig. 5**G, H**); 'median dorsal' for the anterior median dorsal plate of antiarchs (AMD, Fig. 3**C, D**; the posterior median dorsal is supposed to be secondarily incorporated from behind); and 'posterior median ventral' for the median ventral plate of antiarchs (MV, Fig. 5**F**).

These homologies have been retained here, and I also accept that a true spinal is present in rhenanids (Figs 5**G, 7I**), even if it is fragmented or covered with tesserae.

On the other hand, I will not follow Miles and Young's suggestions on the following five points:

i) the supposed absence of posterolateral plates in Acanthothoraci (Fig. 4**A, B**). This plate has not been recovered in any acanthothoracid, but its existence or the presence of a topographically equivalent element is witnessed by a clear contact face on the posterior part of the anterior lateral plate in *Palaeacanthaspis* (Fig. 4**B**; Stensiö, 1944: fig. 4B) or *Weejasperaspis* (White, 1978: fig. 5), and an overlapped area on the posterior dorsolateral plate of *Kosoraspis* (Fig. 4**A**; Gross, 1959: fig. 8). In other forms, it is supposed to be missing (*Romundina,* Ørvig, 1975). Where it has been observed, the overlapped area suggests a very small 'posterolateral' plate, indicating that it may have been a modified scale incorporated in the body armour. In primitive placoderms, as implied by some arthrodires (e.g. *Sigaspis,* Goujet, 1973) and antiarchs (Lyarskaya, 1981: fig. 36), the tail may have been covered with large scales.

ii) the distribution of posterior ventrolateral plates. According to Miles and Young these are present only in arthrodires, antiarchs and phyllolepids (PVL, Fig. 5**A, B, F**), suggesting a common ancestry for the three groups. They deny that a true posterior ventrolateral exists in petalichthyids, rhenanids and acanthothoracids, all groups in which such a plate can be assumed on positive evidence.

In petalichthyids, Miles and Young (1977: 130) interpret the plates situated just behind the anterior ventrolateral plates in *Lunaspis* (Fig. 5**D**) as modified scales like

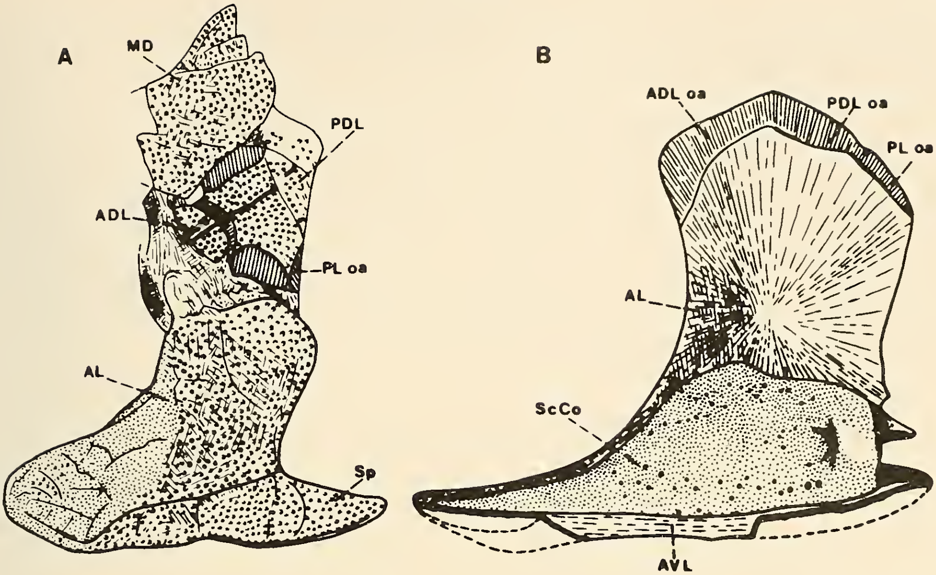

Fig. 4. **A**, *Kosoraspis peckai*, lateral view of the body armour, from Gross (1959). × 0.6. **B**, *Pataeacanthaspis vasta*, inner view of the endoskeletal shoulder girdle and its dermal cover, from Stensiö (1944). × 1.5.

those behind the trunk armour in *Sigaspis* (Goujet, 1973: fig. 2). This raises the question of how a 'true' posterior ventrolateral plate may be characterized. Miles and Young argue that there is also no posterior median ventral plate in *Lunaspis,* but in the only specimen (Fig. 5**D**) showing the ventral part of the body armour, the area of the posterior median ventral is apparently imperfectly prepared (Gross, 1961: pl. 5), or badly preserved. In *Wijdeaspis,* the visceral surface of the anterior ventrolateral plate (Heintz, 1937: pl. 1, fig. 5) clearly shows fine radiating striations around the mesial bone margins characteristic of overlap areas, including the zones corresponding to those for the posterior median ventral and posterior ventrolateral in arthrodires. Either the posterior median ventral plate was present in petalichthyids, or the corresponding space in *Lunaspis* was open, or covered by scales. But both these alternatives seem very unlikely, as these conditions are not known in other placoderms. The possibility that *Lunaspis* had a median ventral opening in the trunk armour is also contradicted by the high degree of ossification of the dermal armour in this genus.

Regarding the lack of data on a posterior ventrolateral plate in other petalichthyids, I point out that complete articulated individuals are known only in *Lunaspis. Macropetalichthys* from North America and China (Stensiö, 1925; Pan, Wang and Liu, 1975), and *Wijdeaspis* from Spitsbergen (Heintz, 1937) and USSR (Obruchev, 1964: pl. 1, figs 1, 2, 4) are only known from disarticulated elements. Among the *Macropetalichthys* material I have examined in various North American collections, the proportion of body plates to the number of skulls is very low. This may be the result of selecting out the most spectacular specimens, during the sporadic discoveries of the 19th century. Only the anterior ventrolateral, spinal and anterior lateral plates are common in museum collections.

As a conclusion, I accept Gross's (1961) interpretation of *Lunaspis* (Fig. 5**D**) as a model for petalichthyids. The plate named posterior ventrolateral (PVL) is a strict homologue of the one in arthrodires and phyllolepids. It even presents the peculiar S-shaped suture between the right and left plate which characterizes this contact in some arthrodires (*Arctolepis,* Fig. 5**A**; *Tiaraspis,* Gross, 1962a). This interpretation has been argued by Young (1980: 63) who reaches almost the same conclusion.

However, I do not follow either Gross's or Young's interpretation of the small paired plate situated immediately behind the posterior ventrolateral plate. Gross (1961: fig. 5) calls it a 'posterior ventral' plate, and considers it as an exclusive feature of petalichthyids (or of *Lunaspis*). Young (1980: 64) considers it to be the posterior part of the posterior ventrolateral; he interprets the transverse linear feature on the specimen not as a suture, but as the external expression of an inner transverse ridge inferred to encircle the body armour as in antiarchs and dolichothoracids (*Dicksonosteus,* Goujet, 1975). In my opinion, this small plate is not strictly part of the body armour; by comparison with *Sigaspis* (Goujet, 1973: fig. 1), it would seem to represent a dermal cover for the pelvic girdle.

Thus, the only differences between the posterior ventrolateral plate in *Lunaspis* and in arthrodires and antiarchs seem to be its smaller size, and an apparent lack of a lateral ascending lamina forming part of the side of the armour. It is relevant to note that the posterior ventrolateral plate in phyllolepids also lacks a lateral lamina, and I suggest that its absence is a plesiomorphic state, a proposal supported by the interpretation of the body armour of rhenanids and acanthothoracids.

In rhenanids, Miles and Young (1977) also concluded that a posterior ventrolateral was absent (cf. Stensiö, 1959, 1969). Miles and Young refer to *Gemuendina* (Fig. 5**G**), which has been interpreted in two different ways. Posterior ventrolateral plates were reconstructed by Stensiö (1959: figs 13, 14, 16) but this was not accepted by Gross (1963: 58). *Gemuendina,* like all the material from the Hunsrück shales, remains extremely difficult to interpret, and the question cannot be answered with such material. However, in *Jagorina* (Fig. 5**H**) there is clearly a separate plate in the same position as the posterior ventrolateral plate on the only specimen known (Stensiö, 1959: fig. 60), which cannot be confused with a bony process of the anterior ventrolateral as in the case of *Gemuendina.* This plate is very small, compared to its homologue in arthrodires or antiarchs. Moreover, there is no midline contact between the left and right plates, and the ventral side of the trunk armour is widely embayed from behind. Nevertheless, I interpret this plate as a posterior ventrolateral homologous to that in arthrodires, antiarchs, phyllolepids, and petalichthyids.

The posterior ventrolateral plate in acanthothoracids was not considered by Miles and Young, but the anterior ventrolateral of *Romundina* has a clear overlap area (PVLoa, Fig. 5**E**; Ørvig, 1975:pl. 4, figs 2, 4) which suggests a plate in the same situation as the posterior ventrolateral of *Jagorina.* More complete acanthothoracid material is needed to confirm the size and shape of this plate, but in my opinion the evidence of the overlap area is sufficient to demonstrate its existence in this group.

iii) On the distribution of the interolateral plate among placoderms, Miles and Young (1977: 130, table 1) accept its presence in five groups (arthrodires, phyllolepids, petalichthyids, acanthothoracids and pseudopetalichthyids). In the last three groups, however, the presence of such a plate is questionable. The pseudopetalichthyids are too

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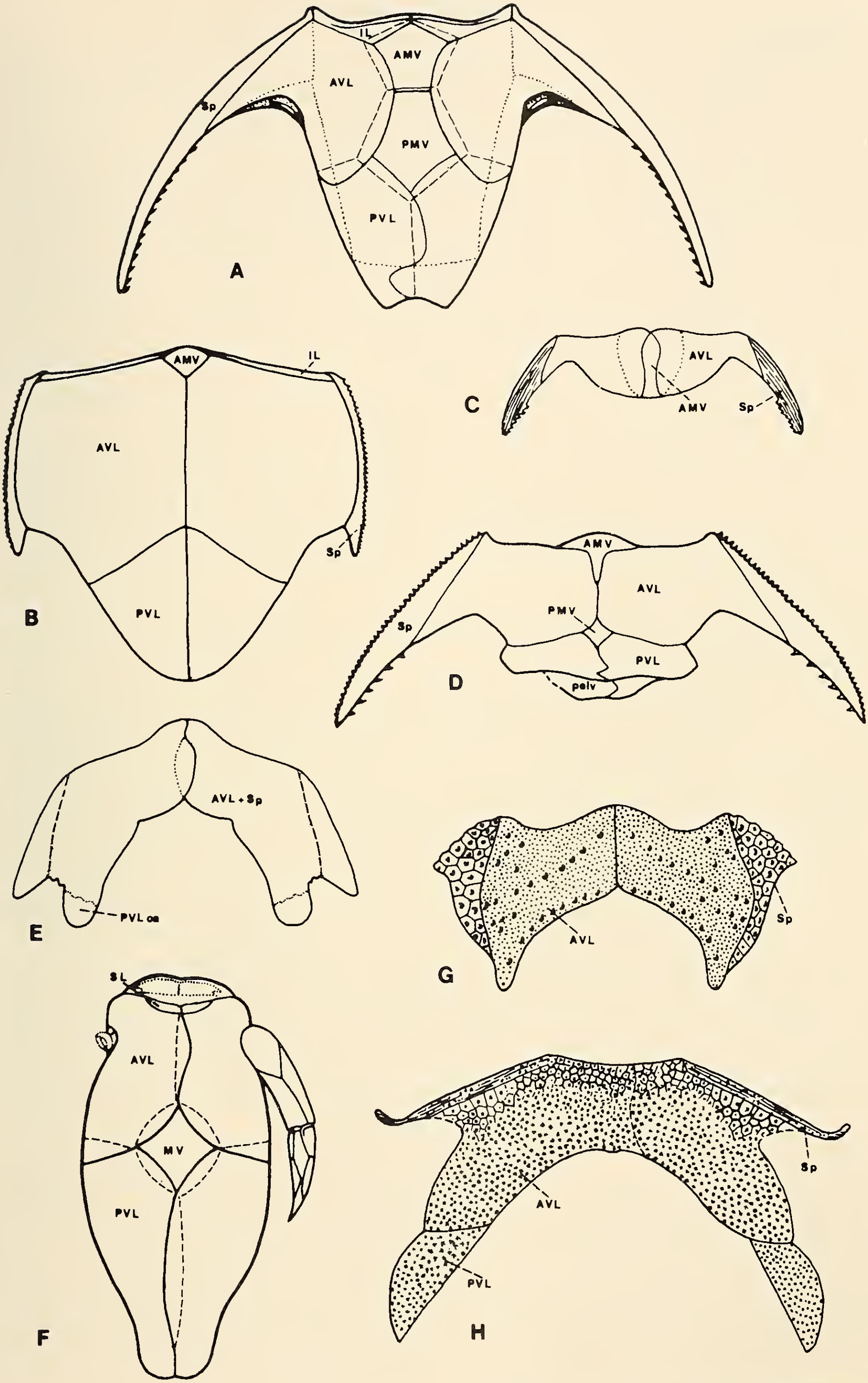
Fig. 5. Ventral view of the trunk shield in representatives of the various placoderm groups. **A**, phlyctaeniid arthrodire: *Arctolepis decipiens.* × 0.45. **B**, phyllolepid: *Phyllolepis orvini,* from Stensiö (1959). × 0.4. **C**, ptyctodontid: *Rhamphodopsis threiplandi,* from Miles (1967). × 2.3. **D**, petalichthyid: *Lunaspis broilii,* from Gross (1961). × 0.4. **E**, acanthothoracid: *Romundina stellina,* modified from Ørvig (1975). × 2.2. **F**, antiarch: *Asterolepis maxima,* from Traquair (1914). × 0.2. **G**, rhenanid: *Gemuendina stuertzi,* from Gross (1963). × 0.6. **H**, rhenanid: *Jagorina pandora,* redrawn from Stensiö (1959). × 0.6.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PMV
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B
AMV
IL
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C
AVL
AMV
Sp
D
AMV
AVL
PMV
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PVL
pelv
E
AVL+Sp
PVL oa
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AVL
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F
SL
AVL
MV
PVL
H
AVL
Sp
PVL

poorly preserved for meaningful discussion, but there is better evidence regarding petalichthyids.

In *Lunaspis,* Gross (1961) made a point of delineating the interolateral plate with dotted lines, and this plate has never been identified in any other petalichthyid, even in those specimens where the anterior ventrolateral plate remains in close association with the spinal plate. Thus, I consider that the interolateral plate is absent in petalichthyids.

In Acanthothoraci, the same plate has been reconstructed in *Palaeacanthaspis* by Stensiö (1944: fig. 4B), in *Romundina* by Ørvig (1975: fig. 4A), and in *Brindabellaspis* by Young (1980: fig. 21). These three authors have again delimited the plate by dotted lines, the area supposed to correspond to the interolateral plate being indistinguishable from the anterior ventrolateral. In the absence of clear evidence I do not admit a separate interolateral plate in Acanthothoraci.

To summarize, only in arthrodires (Fig. 5**A**) and phyllolepids (Fig. 5**B**) is the interolateral a definite separate plate, with its own centre of radiation. This plate can also be characterized by the presence of a wide transverse groove on its ventral surface.

iv) The plate classically called anterior ventrolateral in antiarchs includes, in my opinion, an anterolateral component which dorsally encloses the pectoral fenestra (Jollie, 1962: fig. 6-70). In fact, the antiarchs seem to possess a single plate covering the scapulo-coracoid, whether it is called an anterior ventrolateral, or considered as an integrated complex including spinal and anterolateral elements. In no antiarch are these components clearly delimited, even if, in yunnanolepids (Fig. 3**D**; Zhang, 1978) a spinal process is present.

This single unit, with no sutures between the plates covering the endoskeletal shoulder girdle, seems to be an exclusive feature of the antiarchs, and can be retained as a good apomorphy for the group.

In some respects, a similar situation is met with in Acanthothoraci, although the spinal, anterolateral and anterior ventrolateral plates still remain as distinct components. In *Palaeacanthaspis* (Stensiö, 1944), the sutures between the spinal and both other plates can be drawn from the change in orientation of the radiating internal tubules of the bone. In *Weejasperaspis* (White, 1978), they are suggested by the distribution of ornamental ridges or rows of tubercles. In forms where the ornament is evenly distributed, the sutures are more difficult to set out. In *Brindabellaspis* (Young, 1980) only the posterior end of the suture between the spinal and the anterolateral has been clearly seen. In *Romundina,* the suture between the spinal and anterior ventrolateral plates can be observed on a single specimen (Ørvig, 1975: pl. 5, fig. 6), thanks to the wear of the bone surface. Therefore, at first sight, the 'pectoral cover' in *Romundina* and *Brindabellaspis* might be regarded as a single plate, as in antiarchs (see also Mark-Kurik, 1974: fig. 8). It differs mainly in its large post-branchial lamina, which is absent in antiarchs. More typically, the pectoral cover appears to be composed of two elements (*Weejasperaspis, Palaeacanthaspis, Kosoraspis;* Gross, 1959: fig. 8, and possibly *Radotina kosorensis*), the anterolateral area being divided from the ventral shield (spinal and anterior ventrolateral plates) by a distinct suture.

If a high cohesion of the pectoral cover is a seemingly common feature amongst Acanthothoraci, it does occur also to a lesser extent in forms where the plates exist as separate units. In such cases they remain articulated when fossilized. This is the case in actinolepid arthrodires (see Stensiö, 1944: fig. 15), ptyctodontids, petalichthyids, and rhenanids. As in some Acanthothoraci, the anterolateral plate often separates more easily than the components of the ventral unit, namely the spinal, anterior ventrolateral, interolateral (when present) and anteroventral plates (the last in actinolepid arthrodires only).

I consider the cohesion of the ventral unit as a character which may correspond to

	MD	ADL	AVL	AL	Sp	PVL	PDL	PL	AMV	PMV	IL	AV	dermal pectoral unit
ACANTHOTHORACI	1	1	1	1	1	1	1	1	?	0	0	0	1,0
ANTIARCHS	1	1	1	0	1,0	1	1	1	0	1	0	0	1
ARTHRODIRES	1	1	1	1	1	1	1	1	1	1	1	1,0	0
PETALICHTHYIDS	1	1	1	1	1	1	1	0	1	1	0	0	0
PHYLLOLEPIDS	1	1	1	1	1	1	0	0	1	0,?	1	0	0
PTYCTODONTIDS	1	1	1	1	1	0	0	0	1	0	0	0	0
RHENANIDS	1	1	1	1	1	1	0	0	?	0	0	0	0

Fig. 6. Distribution of plates in the armour of individual placoderm groups.

the primitive condition in the placoderms, but the firm relationship between the anterolateral plate and the ventral unit, with partly synostosed sutures as seen in *Brindabellaspis* or *Romundina,* is likely to be a secondary specialization.

v) The anterior median ventral was regarded by Miles and Young (1977) as a primitive component of the placoderm trunk armour, but this plate has never been found in Acanthothoraci, although an articulated body armour is not known in this group, and the overlap area seen medially on the anterior ventrolateral might be for this element. In rhenanids, an anterior median ventral has been included by Stensiö (1959: fig. 60) in *Jagorina,* as an element fused with the right anterior ventrolateral. However an anterior median ventral is lacking in *Gemuendina,* and given the available data on *Jagorina,* the presence of such a plate in this group is uncertain.

Relevant here is the interpretation of the semilunar plate of antiarchs, and whether it is homologous with the anterior median ventral of arthrodires, as assumed by Miles and Young (1977). On morphological grounds, there are no striking differences between this plate and the unpaired semilunar of bothriolepid antiarchs. However, an unpaired semilunar is restricted to bothriolepids and a few asterolepiforms (e.g. *Gerdalepis*) amongst the antiarchs. This condition can therefore be interpreted as derived, relative to the paired semilunars of other asterolepiforms, sinolepids, and yunnanolepiforms, where they are rather large plates (see Zhang, 1978: fig. 1). In this case, the primitive antiarch condition shows that homology with the anterior median ventral cannot be accepted. The alternatives are that the semilunar is either homologous with the interolateral of arthrodires (Stensiö, 1969: 517), or is a special plate restricted to the antiarchs. I do not accept the first alternative for morphological reasons (the semilunar has no postbranchial lamina), and I provisionally suggest therefore that the semilunar plate is a special apomorphy of antiarchs.

The discussion on these five points just presented leads to a reconsideration of Miles and Young's (1977) table of the distribution of the homologous plates in the body armour of the various placoderm orders. My conclusions are summarized in Fig. 6.

From this table, the primitive morphotype of the body armour may be inferred as a pair of composite bones (with an anterolateral, spinal, and anterior ventrolateral) covering the endoskeletal shoulder girdle, associated with a single median dorsal, paired anterior and posterior dorsolateral, and paired posterior ventrolateral plates. The flanks were open behind the pectoral fin articulation. The posterolateral plate exists in antiarchs and arthrodires, but also in Acanthothoraci. It cannot be kept as a synapomorphy of the two former groups, and could also be a component in the ancestral state of the armour. If so, the absence of a posterolateral in phyllolepids, petalichthyids, ptyctodontids, and rhenanids, would be secondary.

The pectoral fenestra is unique to antiarchs and arthrodires, but the surrounding plates are different, so it cannot be regarded as homologous between the two groups. The posterior ventrolateral plate which accompanies the closure of the flanks of the armour behind the pectoral fenestra has been considered by Miles and Young and Denison as a shared specialization of antiarchs and arthrodires, but the presence of such a plate in some Acanthothoraci and rhenanids devalues this character.

The presence of an interolateral as a separate unit only in arthrodires and phyllolepids suggests a closer relationship between them. Otherwise, the body armour composition provides little evidence on the interrelationships of the other groups. However, the fused dermal pectoral unit in *Brindabellaspis* and *Romundina* would support a closer relationship of these acanthothoracids with the antiarchs.

THE SKULL ROOF PATTERN

At first glance, the characters concerned with the skull roof are more difficult to use than those of the body armour. The analysis of the significance of tesserae and paranuchal plates given by Miles and Young (1977) well illustrates this difficulty; on neither point could a preferred hypothesis be demonstrated by these authors.

Regarding the skull roof dermal bone pattern (Fig. 7), I agree with Denison that this feature should be used with caution in assessing relationships. In fact, our present knowledge of placoderms shows that a fixed bone pattern in one group can only be easily interpreted with reference to that of another by invoking fusion-fragmentation processes, or intermediate states, as numerous as are necessary to effect the required transformation. This is hardly a testable procedure.

Yet, as Denison has noted, the absence of fixed relationships between the skull roof bones and to the sensory canal pattern might be a plesiomorphy in placoderms. In other words, the primitive condition of the skull roof would correspond to an unstable bone pattern. The best examples of such a labile state can be found in the tesserate forms, mainly the Acanthothoraci. By comparing the known skull roofs of *Radotina* (Gross, 1958, 1959) or *Kosoraspis* (Gross, 1959) it is clear that almost all show, in a similar skull roof pattern, a different extent of plates and tesserate areas. These observations have led me to reconsider two problems already analysed by Miles and Young (1977), namely the phyletic significance of tesserae, and of the number of paranuchal plates.

Considering first the meaning of tesserae, one point needs clarification; 'tesserae' *sensu stricto* are superficial elements superimposed on the dermal plates (Gross, 1959; Westoll, 1967), as in *Kimaspis* (Mark-Kurik, 1973). They should not be confused with dermal plates of small size. This important distinction could be analysed further to resolve much misunderstanding, but this is beyond the scope of the present study. Here, I use the term tesserae in the sense of Gross (1959) and Stensiö (1963, 1969). As Miles and Young (1977) have pointed out, if tesserae are interpreted as secondary structures, a reversal in the evolution of some groups towards a supposed micromeric ancestral state must be considered. If, on the contrary, tesserae are considered as a plesiomorph state, this implies their disappearance at least in three groups of macromeric placoderms: arthrodires, antiarchs, and some acanthoracids. In the last group, tesserae are absent in *Romundina* (Fig. 8**C**; Ørvig, 1975), *Palaeacanthaspis* (Stensiö, 1944), and *Radotina prima* (Fig. 9; Gross, 1958).

The parsimony principle does not permit a reasonable choice between these hypotheses, yet Miles and Young favoured the first, that tesserae are a secondary feature. They noted that the body armour in most placoderms is made of large plates, and the thoracic tesserae which occur only in rhenanids can thus be seen as secondary,

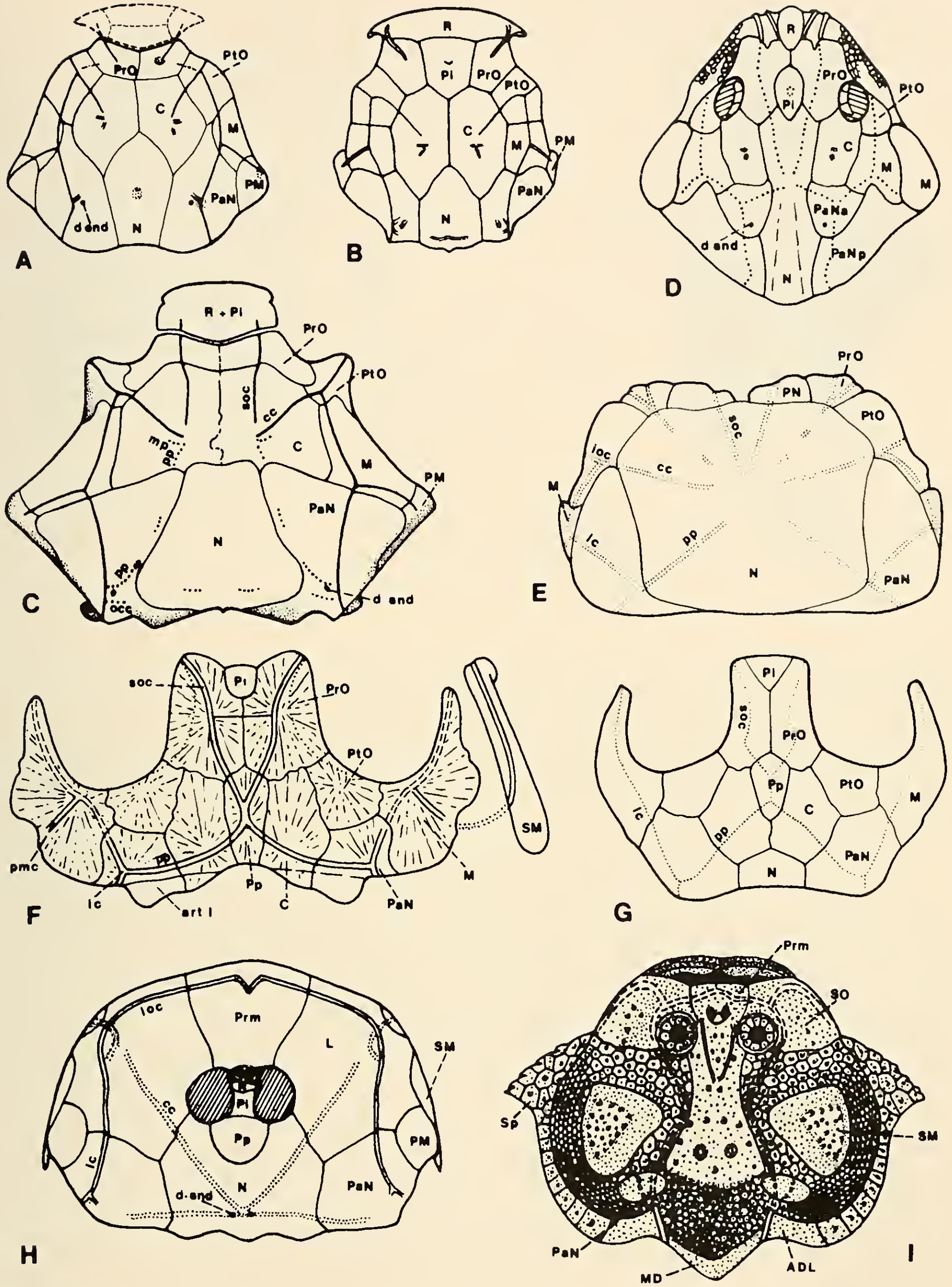


Fig. 7. Cranial shield of various placoderms, dorsal view. **A**, actinolepid arthrodire: *Kujdanowiaspis* sp., modified from Denison (1958). × 0.6. **B**, phlyctaeniid arthrodire: *Arctolepis decipiens,* from Goujet (1975). × 0.6. **C**, brachythoracid arthrodire: *Buchanosteus confertituberculatus,* from White and Toombs (1972). × 0.35. **D**, petalichthyid: *Lunaspis broilii,* slightly modified from Gross (1961). × 0.5. **E**, phyllolepid: *Phyllolepis orvini,* from Stensiö (1936). × 0.15. **F**, ptyctodontid: *Ctenurella gladbachensis,* from Ørvig (1962). × 2.3. **G**, ptyctodontid: *Rhamphodopsis threiplandi,* from Miles (1967). × 5. **H**, antiarch: *Bothriolepis canadensis,* from Denison (1978). × 0.8. **I**, rhenanid: *Gemuendina stuertzi,* from Gross (1963). × 0.6.

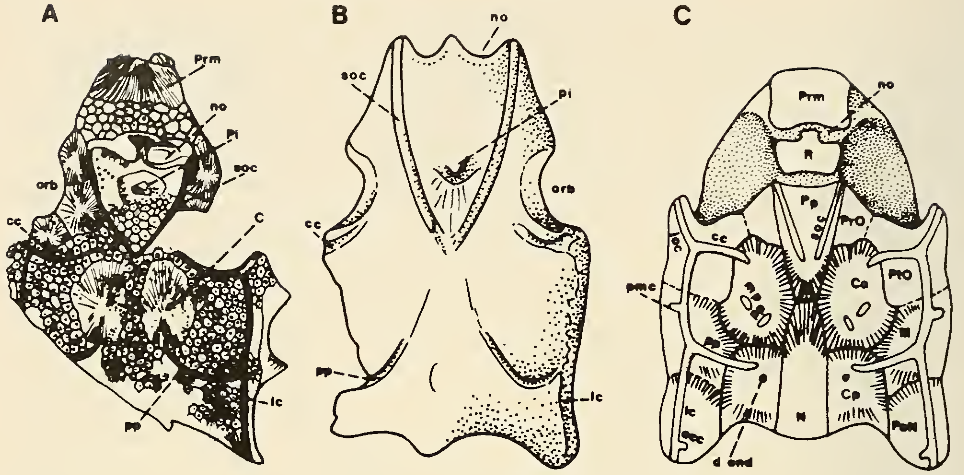


Fig. 8. Skulls of acanthothoracids, dorsal view. **A**, dermal shield of *Radotina kosorensis,* from Gross (1959). × 0.6. **B**, upper surface of the endocranium of *Radotina prima,* redrawn from von Koenen (1895). × 1.3. **C**, cranial shield of *Romundina stellina,* from Ørvig (1975). × 3.

and as a synapomorphy uniting members of this last group. The fact that the pattern of distribution of tesserae on the skull roof is rather similar in gemuendinids and acanthothoracids (Westoll, 1967) reinforces this suggestion.

Accepting this solution would imply that within the Acanthothoraci the tesserate forms would be more closely related to rhenanids than to the non-tesserate acanthothoracids. Thus, this proposal would dismember the Acanthothoraci into two diverging sets.

Also to be considered is the possible presence of tesserae in the petalichthyid *Lunaspis* (Fig. 7**D**). In this fish, a series of platelets covers the anterior part of the cheek, in the position of the suborbital plate of other placoderms. These platelets have been interpreted as tesserae on morphological grounds (Stensiö, 1969; Denison, 1978: 12), but they may not be homologous to the tesserae as they occur in acanthothoracids and rhenanids. Concerning the tesserate acanthothoracids we lack any information on this part of the skull, but in rhenanids (*Gemuendina*; Fig. 7**I**), one of the areas conspicuously devoid of tesserae is the suborbital region. This is covered by a large dermal plate associated with the palatoquadrate (Gross, 1963), as is the suborbital plate of other placoderms. Whereas the distribution pattern of tesserae on the skull of acanthothoracids and rhenanids is rather similar, it differs entirely from that in petalichthyids, as exemplified by *Lunaspis.* I therefore do not consider the suborbital tesserae of *Lunaspis* as any indication of a closer relationship of this fish with the tesserate acanthothoracids and rhenanids, notwithstanding the general similarity of these platelets.

Turning now to the number of paranuchal plates in the skull, the proposal (Westoll, 1967; Miles and Young, 1977) that this depended on the length of the occipital region has not provided conclusive results. It can be noted however that, except for the petalichthyids, more than one paranuchal plate is generally encountered among forms lacking a stabilized skull roof pattern. If these features were considered to be linked, and a variable skull roof pattern is accepted as a plesiomorphy, it follows that two paranuchals is also likely to be the primitive condition.

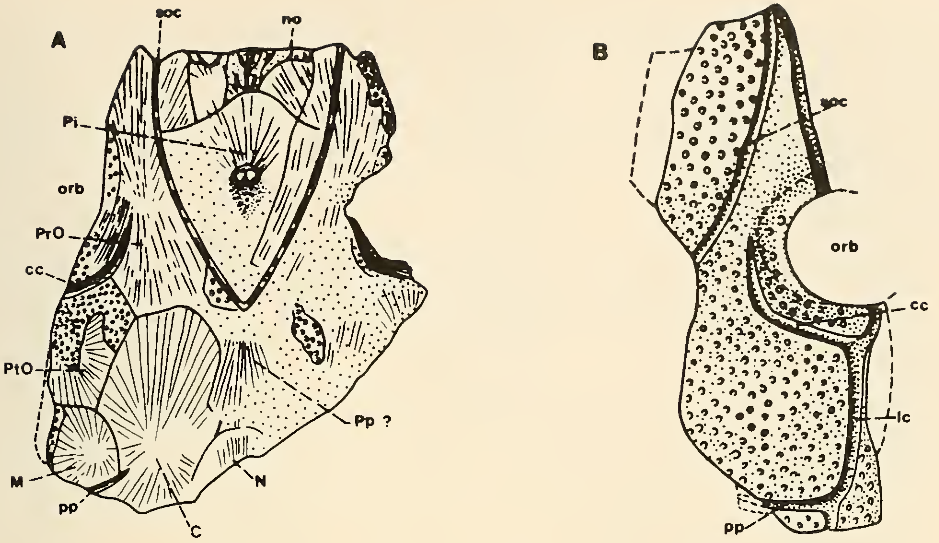


Fig. 9. **A**, *Radotina prima,* incomplete skull with part of the dermal bone preserved. × 1.5. **B**, *Radotina* sp., positive cast of the anterior half of a skull, from Gross (1958). × 0.75.

In petalichthyids, the primitive feature of two paranuchals has persisted, but on the anterior paranuchal three special structures are associated: the posterior pit-line, the main lateral line, and their junction in front of the endolymphatic foramen. This association on the same paranuchal plate is found elsewhere only in the arthrodires (on the single paranuchal plate), and I suggest that this is a special shared feature of the two groups.

Considering in more detail the position of the endolymphatic opening, two main patterns occur in placoderms:

a) The external foramen may be almost directly above the endocranial opening. This means the dermal part of the endolymphatic canal is short, and both internal and external openings are close to the mid-line of the skull. This condition occurs in antiarchs (e.g. *Bothriolepis,* Fig. 7**H**; Stensiö, 1948: figs 9, 12; *Asterolepis,* Karatajute-Talimaa, 1963: figs 2, 7), acanthothoracids (*Romundina,* Fig. 8**C**; Ørvig, 1975: pl. 1, figs 1, 3; *Brindabellaspis,* Young, 1980: figs 1, 2; *Kosoraspis,* Gross, 1959: fig. 6B, D-F), and petalichthyids (*Macropetalichthys,* Stensiö, 1969: figs 21, 130 A, B).

b) The dermal endolymphatic duct is a long oblique tube running in the thickened dermal bone, from the mesially placed endocranial opening to the external foramen, situated far postero-laterally. This occurs only in arthrodires. In all their subgroups the external foramen opens at the radiation centre of the paranuchal plate, behind the distal division of the posterior pit-line, and in front of the occipital line, where these join the main lateral line (Fig. 7**A-C**).

Since this second condition is an exclusive feature of arthrodires, it can be proposed as a synapomorphy supporting the monophyly of the group. By comparison, the first pattern can be regarded as plesiomorphic. Outside the placoderms, in the Osteostraci on the one hand (see Wangsjo, 1952; Janvier, 1980), or in the elasmobranchs on the other, the endolymphatic duct opens near the mid-line, or even by a single median foramen, which supports this interpretation.

I regard an external foramen for the endolymphatic duct as an ancestral primitive character. No trace of such a foramen is shown in ptyctodontids (Ørvig, 1971: 30), and there is also no indication of an endocranial opening. In rhenanids, on the contrary, the internal foramen exists, but no external opening has been noted. From the position of the internal foramen, and if we suppose the duct to be vertical, it should open within the small transverse groove called the 'middle pit-line' in *Jagorina* and *Asterosteus* (Stensiö, 1969: figs 92, 98).

THE POSITION OF THE NASAL CAPSULES, AND THE PREMEDIAN PLATE

Generally open to the front, the endoskeletal nasal capsules in placoderms are covered by a rostral plate which usually bears a medial process separating the incurrent nostrils (see Denison, 1978). They occupy one of the three following positions relative to the orbital cavity:

1) at the extremity of a well-developed endocranial ethmoidal region, far in front of the pineal pit. This is the condition in petalichthyids (Stensiö, 1969), the acanthothoracid *Radotina prima* (Figs 8**B**, 9**A**; von Koenen, 1895: pl. 4, fig. 2; Gross, 1958: fig. 6, pl. 1, fig. 3), and *Radotina* sp. (Fig. 9**B**; Gross, 1958: fig. 6, pl. 3, figs 5, 6).

2) at the end of a short ethmoidal region, where they open ventrally and are covered by a wide rostral plate (arthrodires, Fig. 10**C**).

3) in a posterodorsal position on a well-developed ethmoidal region, and at the anterior limit of the orbital cavity. In this position they open to the front in *Romundina* (Fig. 10**B**) and the antiarchs (Fig. 10**A**), or to the front and slightly upwards in *Radotina kosorensis* (Fig. 8**A**) and rhenanids (Fig. 10**D**).

Where a well-developed endocranial 'rostrum' is present, its dermal cover varies. In case 1 it is composed of a small and more or less elongated rostral plate (*Lunaspis,* Fig. 7**D**, or *Wijdeaspis,* see Heintz, 1937; Obruchev, 1964:pl. 1, fig. 1). In case 3 there is a prerostral plate — called a premedian, after the antiarch terminology — which is generally short in acanthothoracids (*Romundina,* Fig. 10**B**; Ørvig, 1975: pl. 3, fig. 4; *Radotina kosorensis,* Fig. 8**A**; Gross, 1958: fig. 1) and in most early antiarchs (see Janvier and Pan, 1982), but longer in bothriolepids (see Stensiö, 1948; Long, 1983). In his original description of *Radotina kosorensis* Gross interpreted the plate in a prerostral position as a rostral; this interpretation was followed by Denison (1975: fig. 3), but the plate was renamed a premedian by Denison (1978).

Three morphological transformation sequences can be proposed to account for these three conditions:

Hypothesis A: Anteriorly-placed nasal capsules, opening to the front (state 1 above) was the ancestral condition, and states 2 and 3 represent diverging specializations.

Hypothesis B: State 2, with the nostrils opening downwards, was ancestral. The nostrils opening to the front (state 1) was an intermediate state, and posteriorly-situated nasal capsules (state 3), was the ultimate specialization.

Hypothesis C: Posteriorly-situated nasal capsules (state 3) was ancestral, terminal capsules (state 1) was an intermediate condition, and nostrils opening ventrally (state 2), was the most specialized condition.

By reference to the most general condition in gnathostomes, we may test which of these three solutions is most parsimonious, which does not mean of course that it is correct, but only the most reasonable preliminary proposal. Tests to falsify these hypotheses must be inferred from other combinations of characters exhibited by other forms, and using parsimony as a strict methodological principle. Accordingly, I apply the same 'rule' as Miles and Young: I will be more inclined to accept a multiple independent loss of a bone than its multiple origin.

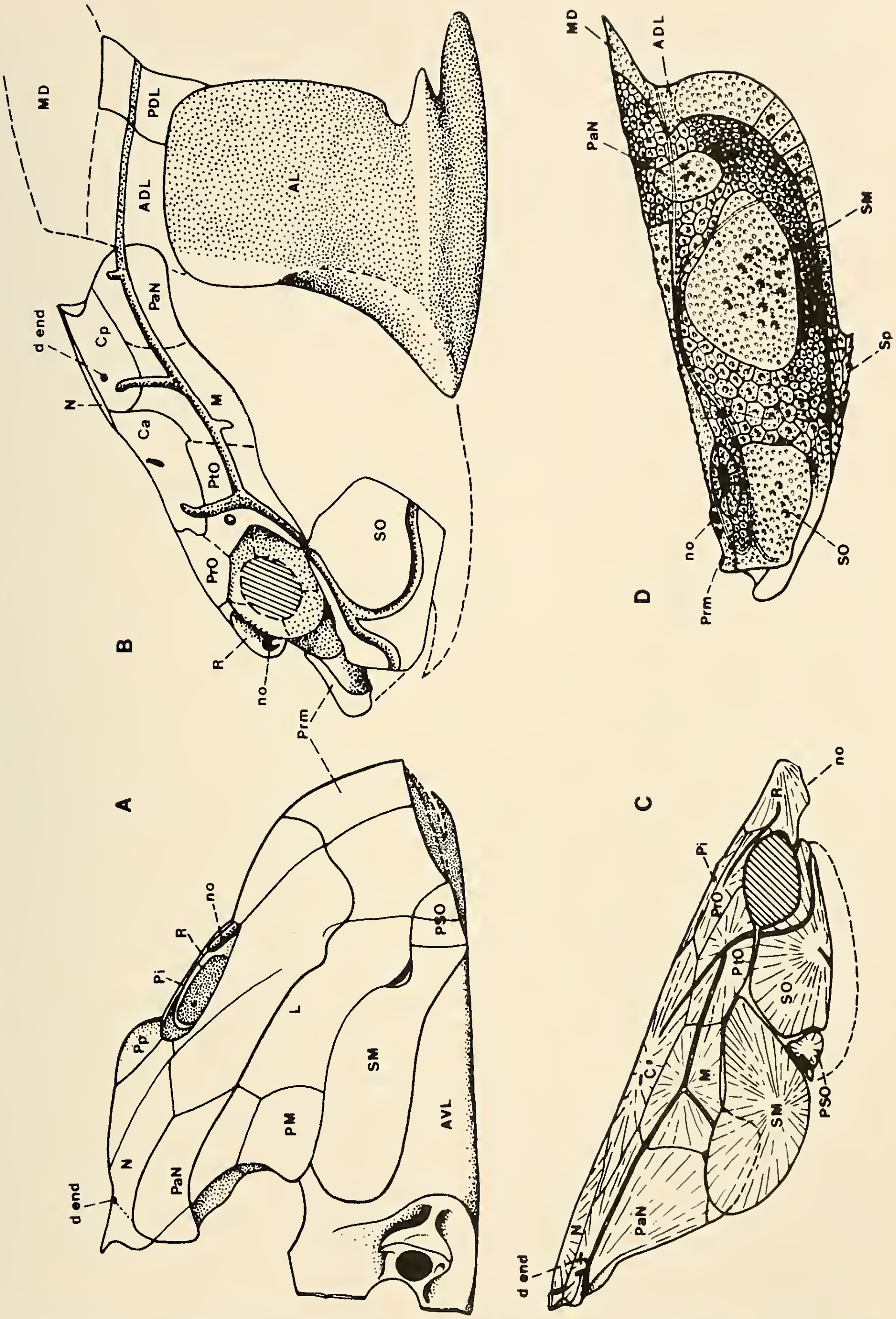


Fig. 10. Lateral view of the skull. **A**, antiarch: *Bothriolepis canadensis,* from Stensiö (1948). × 1. **B**, acanthothoracid: *Romundina stellina,* after Ørvig (1975). × 2.8. **C**, arthrodire: *Arctolepis decipiens,* from Goujet (1972). × 1.2. **D**, rhenanid: *Gemuendina stuertzi,* modified from Stensiö (1969). × 0.35.

Given these conditions, hypothesis B is less parsimonious. It requires a development of the subnasal shelf of the endocranium, then the backward regression of the nasal capsules, and the formation of a new plate, the premedian, to cover the dorsal face of the ethmoidal subnasal shelf.

Hypotheses A and C are equally parsimonious insofar as they imply only bone regression. However I dismiss hypothesis C because dorsal or anterodorsal nasal capsules is an extremely rare occurrence among gnathostomes, even if it is a general case in osteostracans. Moreover, there is no indication of a premedian plate in state 1 above (terminal nasal capsules on an endocranial 'rostrum'), even if Denison (1978: fig. 22C) has reconstructed such a plate in *Radotina prima* (but see Figs 8**B**, 9).

It could be objected that a prerostral ('premedian') plate exists in arthrodires, where it is called the internasal plate (see *Coccosteus,* Miles and Westoll, 1968). However, to my knowledge, this plate is absent in nearly all dolichothoracids and a number of brachythoracids, and therefore may have arisen within the group.

I conclude that hypothesis A is the preferred solution. It supposes two diverging specializations from an ancestral state with an endocranial 'rostrum' and terminal nasal capsules opening to the front. The implication that the ventral nostrils in arthrodires is specialized is supported by the fact that the ethmoidal region of the endocranium in actinolepid arthrodires (see *Kujdanowiaspis*, Stensiö, 1963: fig. 14) or some primitive brachythoracids (*Buchanosteus*, White and Toombs, 1972; Young, 1979: fig. 2) has a rather long subnasal shelf. A trend toward shortening of this region can be deduced from the evolution of several lineages inside the group. This is well illustrated by *Dicksonosteus* (Goujet, 1975: fig. 4), in which the internasal wall is covered ventrally by a narrow internasal lamina which represents the most anterior point of the ethmoidal endocranial region, notched laterally by the ventral nostrils.

The dorsal position of the nostrils in rhenanids could be considered a result of the 'pseudobatoid' adaptation which characterizes the group. However, the antiarchs and the species of *Radotina* which share this character do not show this specialization in body shape, and their high armour and lateral eyes do not seem particularly well adapted for life on the bottom. This supports the hypothesis that a large premedian plate and the backward shifting of the rostral plate is a special synapomorphy for a group composed of the antiarchs, rhenanids and acanthothoracids with the exception, among the latter, of *Radotina prima,* a form which also lacks tesserae. Thus, the contradiction already noted regarding the significance of tesserae applies again. If we accept posterodorsal nasal capsules and the premedian plate as synapomorphies, this again implies that the Acanthothoraci is not a monophyletic group.

To summarize, by combining the various characters already discussed (tesserae, premedian plate, position of the nasal capsule), three groups can be distinguished within the Acanthothoraci, characterized as follows:

Group 1: no tesserae, a long preorbital region of the skull with terminal nostrils, but no premedian plate. This is the case in *Radotina prima* only.

Group 2: no tesserae, a long preorbital region of the skull covered by a premedian plate, and nasal capsules in a posterior position (just in front of or between the orbits). Examples are *Romundina, Palaeacanthaspis, Brindabellaspis*(?).

Group 3: tesserae, a long preorbital region of the skull covered by a premedian plate, and nasal capsules posteriorly placed. Examples are *Radotina tessellata, R. kosorensis, Kosoraspis peckai, Kimaspis*(?).

The interpretation as synapomorphies of the characters discussed above implies that members of group 3 are related to the rhenanids, which share the same three characteristics, but with tesserae as their only synapomorphy. Group 2 may be more closely related to the antiarchs; the presence of a transverse groove on the posterior part of the premedian of *Romundina,* similar to the preorbital depression of early antiarchs (Janvier and Pan, 1982: fig. 8), is proposed as a synapomorphy supporting this sister-group relationship. This leaves Group 1, which is characterized only by primitive features, and for which no precise relationship can be proposed to other groups of placoderms.

THE CERVICAL JOINT

The dermal cervical joint, its variations, and their phylogenetic implications, were discussed by Miles and Young (1977: 138-139). They concluded that the ginglymoid joint in phlyctaenioid arthrodires (phlyctaeniids and brachythoracids), ptyctodontids, and antiarchs, were independently acquired. They also supposed that 'primitive' arthrodires, as in several other placoderm groups, had no dermal joint, and that the 'sliding joint' and the ginglymoid joint developed within this group as diverging specializations (Miles, 1973). This is contrary to Denison's (1975) view that the ginglymoid joint was possibly derived from the sliding joint.

The dermal cervical joint has been identified, in one form or another, in arthrodires, phyllolepids, antiarchs, ptyctodontids, and petalichthyids. On the other hand, it has not been demonstrated in rhenanids, most acanthothoracids, stensioellids, and pseudopetalichthyids. For the reasons advanced above (p.213) I will not consider the last two groups.

In rhenanids, the probable absence of a cervical joint may be a secondary state, related to the extension of tesserated areas, since the presence of a joint presupposes a certain rigidity of the back of the skull. In *Gemuendina* (Figs **7I**, **10D**; Gross, 1963: fig. 1) one or two rows of tesserae lay between the anterior dorsolateral plate and the small plate supposed to represent the paranuchal. If the tesserae are the result of a secondary bone fragmentation, then the lack of a joint would also be the result of a regressive process. This might be confirmed by looking at the condition in the groups supposed to be most closely related to rhenanids. Under Miles and Young's (1977) and Young's (1980) hypotheses, the Acanthothoraci are this sister-group, but if tesserae are regarded as a uniquely derived character, only tesserate forms can be members of this sister-group, namely *Radotina kosorensis, R. tessellata, Kosoraspis,* and (?) *Kimaspis.* The material of these forms (Gross, 1958, 1959; Mark-Kurik, 1973) provides no evidence of the structure of the cervical joint. It can be noted however that in the Acanthothoraci, the paranuchal projects backwards, and the posterior skull roof margin is embayed. This has been considered a possible synapomorphy of the group (Young, 1980: 67). In *Romundina* (Ørvig, 1975: pl. 1, fig. 3), the visceral surface of the posterior expansion of the paranuchal shows a rough surface which indicates an articular contact with the anterior dorsolateral plate. This plate is unknown in this form, but we can suppose the presence of an articular lamina on the body armour. This point needs clarification with new material, but I consider the cribrosal surface on the paranuchal plate as a positive argument supporting the hypothesis of a sliding articulation in *Romundina.* In other Acanthothoraci, *Brindabellaspis* shows an articular facet on the posterior endocranial expansion of the skull ('craniospinal process', Young, 1980: figs 7-9) covered dorsally by the paranuchal plate. This is evidence of a lateral articulation. Other evidence is provided by an anterior dorsolateral plate from Kotelny Island assigned by Mark-Kurik (1974: fig. 9a,b) to an undetermined 'arctolepid', because of a supposed articular condyle. But this 'condyle' differs from that of typical arctolepids by a remarkable character: its concave dorsal surface. Moreover, the bone bears an ornamentation of stellate tubercles, a morphological detail mentioned, to date, in Acanthothoraci and rhenanids alone among placoderms. Mark-Kurik (*pers. comm.*) now considers that this plate belongs to an acanthothoracid. Thus, we have another indication of the presence of an articular lamina in this group. This lamina bears a fossa as in antiarchs, and differs from what is seen in actinolepid arthrodires. If we add that a swelling of the articular lamina can be seen on some anterior dorsolateral plates of *Wuttagoonaspis* (Ritchie, *pers. comm.*), it can be concluded that the articular condyle of phlyctaeniid style as well as the armour fossa of antiarchs can evolve from a flange. Consequently, the sliding joint can be regarded as the primitive condition in placoderms.

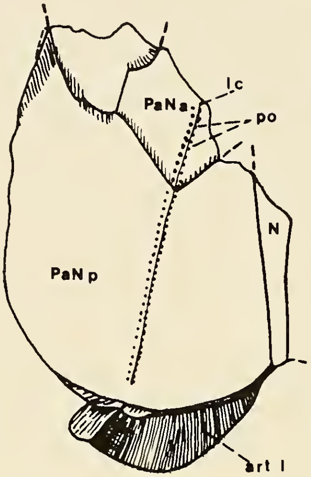


Fig. 11. Macropetalichthys pelmensis, fragmentary skull roof, after Gross (1937). × 0.6.

In petalichthyids, Miles and Young (1977: 138) noted that the cervical joint is hardly understandable due to poor information on the anterior dorsolateral plate. In the Cleveland Museum collections I have studied three anterior dorsolateral plates assigned to *Acantholepis* (BW 3-254, BW 3-238, BW 3-337) showing the articular area. All three have a high articular lamina, exhibiting in front a poorly-developed condyle, which can be interpreted as intermediate between the articular lamina seen commonly in actinolepid arthrodires, and the flat simple condyle of *Wuttagoonaspis*. However, the ascription of these plates to petalichthyids is still controversial. The most interesting phylogenetic information drawn from the cervical joint is given by *Macropetalichthys pelmensis* (Fig. 11; Gross, 1933: pl. 8, fig. 4; 1937: fig. 23B). This form is known by an isolated paranuchal plate which bears a horizontal mesial flange projecting backwards. Such a flange is very similar to the one described in *Ctenurella gladbachensis* (Ørvig, 1960) or *C. gardineri* (Miles and Young, 1977). Although this flange does not carry the articular surface, in both *Macropetalichthys* and *Ctenurella* it forms a posteroventral projection of the thickened posterior margin of the paranuchal plate, which is possibly related to protection of the nuchal gap. This flange may be absent in other petalichthyids, for example *Wijdeaspis warrooensis* (Young, 1978). However this form possesses a dermal cervical joint extremely similar to the one observed in early ptyctodontids (see Mark-Kurik, 1977: fig. 6), particularly in the shape and orientation of the articular fossa, which is longitudinal, contrary to its disposition in arthrodires. Although variation in the cervical joint in petalichthyids needs further investigation, the features recorded above are not seen in other groups to my knowledge, and can be proposed as a synapomorphy of ptyctodontids and petalichthyids. Other shared derived characters of these groups, supporting a sister-group relationship (Fig. 12), are as follows:

1) Their sensory lines are included in tubes which project below the lower surface of the dermal bone, and communicate with the exterior by means of tubules opening on the surface by pores. They also show the same pattern of lines; the supraorbital canal and posterior pit-line canal converge to the centre of the nuchal or 'centronuchal' plate, and the central line is missing (see Ørvig, 1957, 1962, 1971).

Denison (1978: 12, 35) mentions tubular canals and pores in some acanthothoracids (*Kimaspis* and *Kolymaspis*). In *Kimaspis,* the original description (Mark-Kurik, 1973) refers to sensory lines enclosed in the bone tissue, but there is no indication of pores. The structure is very similar to that observed for the main lateral line of the skull in actinolepid and phlyctaeniid arthrodires, where they are represented by a deep groove opening by a narrow slit.

In *Kolymaspis,* Bystrow (1956) does not quote such canals. No precise idea concerning this point is provided by the cast I have studied. However, the widely open supraorbital canal on this skull, and the absence of any indication of pores, suggests that the other sensory lines are presumably not like those in ptyctodontids and petalichthyids. Thus, I consider that tubular canals with superficial pores have not been proved to exist outside these two groups of placoderms. This feature can be kept as a valuable synapomorphy.

2) Ptyctodontids and petalichthyids are the only placoderms where the suborbital and postsuborbital plates are absent, or represented by tiny plates sometimes interpreted as tesserae.

THE PELVIC AND PREPELVIC CLASPERS

Since these organs have been identified only in ptyctodontids they should be of little or no importance for the study of interrelationships inside the placoderms. However Miles and Young referred to them, for they identified only primitive characters or autapomorphies in ptyctodontids, from which it was difficult to build a defensible hypothesis of relationships. They also used the pelvic and prepelvic claspers when comparing the placoderms to other gnathostomes. Their most parsimonious solution, according to the other assumptions of their phylogenetic model, was that ptyctodontids may represent the sister-group of all other placoderms, because they retain the pelvic and prepelvic claspers assumed to have been present in the common ancestor of placoderms and chondrichthyans. Since both categories of claspers have been found only in ptyctodontids and holocephalans, and chondrichthyans are considered to be a monophyletic group, the most parsimonious solution is that the prepelvic claspers have independently disappeared in non-ptyctodontid placoderms and in elasmobranchs. This solution, which explains in the simplest way the clasper distribution, assumes however that pelvic and prepelvic claspers in ptyctodontids and holocephalans are homologous structures. The morphological grounds for this need reexamination.

The pelvic claspers in ptyctodontids are best known. They comprise an exoskeletal plate which covered the copulatory organ, developed, as in chondrichthyans, from the mesial part of the male pelvic fin. This clasper plate has been recovered, in a remarkable state of preservation, in *Rhamphodopsis* (Miles, 1967: fig. 16; pl. 6, fig. 3) and *Ctenurella gardineri* (Miles and Young, 1977: fig. 35). Its ventral position relative to the fin evokes more the elasmobranch condition rather than that of holocephalans (Miles, 1967: 113). This anatomical feature, implying a similar complex reproductive biology, is one of the arguments set out to group placoderms and chondrichthyans as elasmobranchiomorphs (see Miles and Young, 1977; Goujet, 1982). However no sign of such a clasper has ever been found in the other placoderms, and the possibility of their separate origin in ptyctodontids and elasmobranchs, where they show a somewhat different morphology, cannot be excluded. Nevertheless, their possible homology is retained here.

The prepelvic claspers, as interpreted by Ørvig (1960, 1962) and Miles (1967), are represented by a pair of small plates lying in front of the pelvic fin. In *Rhamphodopsis,* where they are best known, each clasper is an elongate dermal plate attached to an endoskeletal ossification. Compared to the prepelvic clasper of holocephalans, however, two important details undermine their possible homology:

i) the prepelvic clasper in holocephalans is an elongated organ, mainly cartilaginous, and normally hidden in a cutaneous pocket. When extracted, it forms a rod bearing on its internal side a series of tiny discrete hooks supposed to be used by the male in grasping and maintaining the female during copulation.

In *Ctenurella gardineri,* Miles and Young (1977: 193) mention a bony plate bearing hooked denticles, which they interpret as a possible prepelvic clasper, although the precise position of this plate on the body is unclear. Supporting their interpretation is the hooked superficial ornament, which evokes the discrete spiny scales of the holocephalan prepelvic clasper. However, both the exoskeletal plate of the male pelvic fin in *Rhamphodopsis* (see Miles, 1967: fig. 19), and the posterior element of the pelvic clasper in *Ctenurella gardineri* (Miles and Young, 1977: fig. 35C, pl. 5A) also bear such hooked denticles. Thus, the ornament in itself cannot be sufficient to retain Miles and Young's suggestion without doubt. Moreover, the small dermal spine interpreted as a prepelvic clasper in *Ctenurella gladbachensis,* as reconstructed by Ørvig (1960: 327, fig. 5), apparently has a rather different morphology. *Rhamphodopsis* is the only form in which the position of the supposed prepelvic clasper is clear, but in this form it is a simple plate of dermal bone showing the same ornamentation as the plates of the armour (see Miles, 1967). If these bones were situated rather deep in the skin, as indicated by the loss of superficial ornament in ptyctodontids, it is impossible to imagine for this 'clasper' the same function of grasping the female during copulation.

ii) The plate supposed to represent a prepelvic clasper in the male is also present in female *Rhamphodopsis,* and was labelled by Miles (1967: fig. 13) as a 'dermal plate lying ventral to the pelvic girdle', a definition which applies also to the male element.

Hence both basic criteria which define the prepelvic clasper in holocephalans are not met in ptyctodontids, where the so-called prepelvic clasper is neither a grasping organ nor restricted to the males. I therefore propose a return to Watson's interpretation (1934, 1938) that these structures simply represent the pelvic girdle. This interpretation, rejected by Miles (1967: 112), implies that the pelvic girdle included a dermal element associated with the endoskeleton. This is contrary to the condition in *Coccosteus* (Miles and Westoll, 1968), and the large majority of gnathostomes, where the pelvic girdle is exclusively endoskeletal. However, an association between the pelvic endoskeletal girdle and a dermal plate has been described in several other placoderm groups, particularly those known by articulated individuals, as in the arthrodires (*Sigaspis,* Goujet, 1973: fig. 2), rhenanids (*Gemuendina,* Gross, 1963: fig. 4), stensioellids (Gross, 1962b: fig. 4), and petalichthyids.

To conclude, I assume that the ptyctodontid 'prepelvic clasper' is only the dermal cover of the pelvic girdle. This exoskeleton may be a primitive condition in placoderms for both pelvic and pectoral girdles. This interpretation is supported by the remarkable fact that all the taxa in which a pelvic exoskeleton has been identified also have a highly-developed scale covering. The lack of a pelvic exoskeleton in *Coccosteus* for example may thus be a secondary condition due to regression of the dermal cover and squamation.

DERMAL BONE HISTOLOGY AND ORNAMENTATION

In placoderms, the dermal plates are composed essentially of two types of hard tissue: bone and semidentine. The bone, which may be either laminar or with primary osteons, makes up the basal and middle layers of the dermal plates. The semidentine is restricted to the superficial layer where it forms the tubercular ornament. This semidentine, containing typical unipolar cell cavities with a long centrifugal apical tubule, is an exclusive feature of placoderms, and a good synapomorphy for the group (Goujet, 1982). However it is largely absent in groups showing regression of the superficial ornament, namely antiarchs (Gross, 1931: fig. 2, pl. 1), phyllolepids (Bystrow, 1957: fig. 25), and some arthrodires (mainly pachyosteomorphs).

Although information is lacking on the histology of many important forms (e.g. ptyctodontids, early antiarchs, *Brindabellaspis*), the available evidence suggests a correlation between the histology of the superficial hard tissue, and the nature of the ornament, which may be of phylogenetic significance. Amongst placoderms the various types of superficial dermal ornament may be organized into five main categories:

1) stellate tubercles showing acute crests, sometimes denticulate, which are separated by deep valleys (Acanthothoraci; see Gross, 1958, 1959; Ørvig, 1975).

2) closely-set flattened tubercles of irregular shape (*Brindabellaspis;* Young, 1980).

3) clear-cut tubercles with either a rounded tip or a 'crown' of dense hard tissue, bearing fine radiating ridges (arthrodires, petalichthyids; see Gross, 1957, 1961, 1962a; Ørvig, 1957, 1971; and possibly *Radotina prima;* Gross, 1958).

4) ridges, either concentric (phyllolepids), radiating, or in an irregular pattern of low ridges and/or blunt tubercles (antiarchs; see Stensiö, 1948; Karatajute-Talimaa, 1963).

5) a smooth or irregular surface, with numerous pores of the vascular canals (ptyctodontids, pachyosteomorph arthrodires).

The histology of the stellate tubercles (category 1), as described by Gross (1973) and Ørvig (1975, 1979), consists of a massive semidentine with few basal vascular canals. Ørvig (1979) calls it orthosemidentine. It has been demonstrated in rhenanids (*Asterosteus = Ohioaspis,* Gross, 1973) and in acanthothoracids (*Romundina,* Ørvig, 1975, 1979). In *Romundina,* this semidentine presents a mixture of unipolar odontocytes and more irregular cavities resembling the sclerocytes of some kind of mesodentine, a common hard tissue outside the placoderms. This tissue can be interpreted in its organization as a semidentine which has kept some characters of a preceding mesodentinous state. From this, we can infer that the thick semidentine present in *Romundina* and the rhenanids may represent a primitive condition.

The histology of *Brindabellaspis* dermal bone is still unknown, but from the massive aspect of the irregular superficial tubercles, it may be predicted that it is probably made of the same type of semidentine as that in the Acanthothoraci.

The ornament of category 3 is more common among placoderms. Its histology shows a semidentine restricted to the peripheral layer at the tip of the tubercles, and surrounding the ascending vascular canals which occupy the core of each tubercle. Ørvig (1979: 234) calls this pallial semidentine, and it seems to be specific to this third type of ornament.

In the ornament of categories 4 and 5, there is only bone tissue. The semidentine has disappeared from the shield plates, but may be retained in the jaw bone.

The phylogenetic significance of the ornament and histology in the placoderms can be analysed as follows. The orthosemidentine and stellate tubercles may be assumed to be the primitive condition, as indicated by the histology observed in *Romundina.* This plesiomorphous state only occurs in acanthothoracids and rhenanids. The pallial semidentine may be seen as a uniquely specialized condition, associated with the crowned tubercles met with in petalichthyids and arthrodires. The same histological structure may also occur in the tubercles of early ptyctodontids (*Tollodus*, Mark-Kurik, 1977), and on the post-branchial lamina of unornamented ptyctodontids, where well-defined tubercles persist (see Miles and Young, 1977: pls 2F, 4A). To date, the histology of these has not been described.

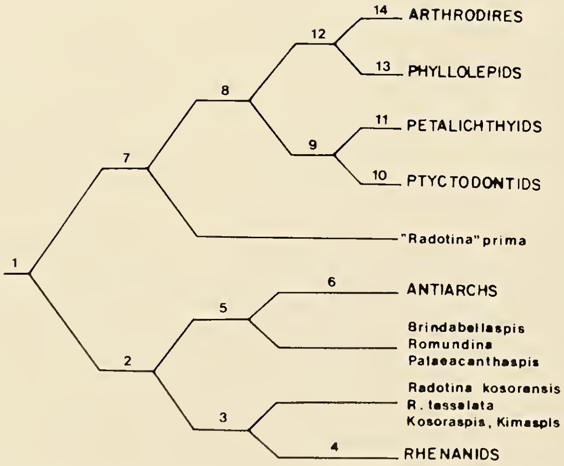
The bony nature of the ornament in a majority of antiarchs, some arthrodires, and phyllolepids, is a secondary regression of the superficial hard tissue, presumably due to a deeper situation of the plates in the skin. This is clearly the case in arthrodires (Stensiö, 1969), and in the antiarchs, where the early forms show an ornamentation of well-defined closely-set tubercles (yunnanolepiforms, Zhang, 1978: pls 4, 5, 8). I suggest that this regressive process has probably occurred independently in each group. Thus it has a low phylogenetic value in the present context.

PLACODERM INTERRELATIONSHIPS: A NEW SCHEME

Using the characters discussed above, the cladogram of Fig. 12 has been set up. It gives a view of placoderm interrelationships which differs to a large extent from those proposed by Denison (Fig. 1) and Miles and Young (Fig. 2).

The placoderm orders are distributed in two major clusters. One groups the arthrodires, phyllolepids, petalichthyids, and ptyctodontids, which share anterior and posterior median ventral plates, and the association, on the same paranuchal, of the endolymphatic foramen and the confluence of the posterior pit-line with the main lateral line (8, Fig. 12). The second cluster groups the rhenanids and antiarchs as major units, which share one uniquely derived character (2, Fig. 12): the dorsal position of the nasal capsules and the presence of a large premedian plate covering the ethmoidal expansion of the endocranium.

This grouping contradicts both Denison's and Miles and Young's phylogenetic schemes, in which the arthrodires and antiarchs are considered as sister-groups using a different synapomorphy (the long body armour with closed flanks behind the pectoral fenestra). This supposed synapomorphy is based on a different appreciation of the distribution of homologous body plates amongst the various placoderm orders. My analysis of these plates, summarized in Fig. 6, shows that most of these plates are present in a majority of the groups taken into account. This assessment is unlikely to change if stensioellids and pseudopetalichthyids were included. Currently these cannot be investigated to the same degree as the other groups.



When applying the parsimony principle, the only plate which can seriously question the proposed cladogram is the median ventral plate of antiarchs, considered as the homologue of the posterior median ventral plate of arthrodires. It is the only plate for which a separate origin must be supposed in antiarchs on one side, and in the most recent common ancestor of arthrodires, phyllolepids, petalichthyids, and ptyctodontids on the other.

The problem may be seen as an opposition between two conflicting synapomorphies: premedian plate and dorsal nostrils *versus* posterior median ventral plate. The first alternative has been preferred here, because in my opinion the multiple origin of the median ventral plate is more likely than the independent occurrence of the competing character. Given the numerous variations in size and form of the median

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Fig. 12. New cladogram for the major placoderm groups (excluding stensioellids and pseudopetalichthyids).

Characters assumed to be basic placoderm apomorphies (1) are: body armour forming a complete ring surrounding the pectoral girdle, and composed of median dorsal, anterior and posterior dorsolateral, anterolateral, spinal, anterior ventrolateral, small posterior ventrolateral and very small posterolateral plates; pelvic girdle covered with a dermal plate; double cervical joint with an endoskeletal component (between occipital condyles and a synarcual) and a dermal component (the posterolateral part of the skull overlapping the front margin of the anterior dorsolateral plate); ornamented layer of the dermal bone made of orthosemidentine; omega-shaped palatoquadrate closely associated with the anterior cheek-plates (suborbital and post-suborbital), with the adductor mandibulae muscle attached on the ventral face of the metapterygoid and the medial face of the suborbital plate; close association between the dorsal hyoid arch elements and the dermal operculum, with the epihyal modified into a simple rod fused to the visceral surface of the submarginal plate, and playing the role of an opercular process joining the dermal cheek to the skull; endocranium composed of two ossifications (rhinocapsular and postethmo-occipital) separated by a fissure, unless secondarily fused; long ethmoid region of the endocranium with terminal nasal capsules and a long subnasal shelf; lateral orbits; variable skull pattern with numerous plates; cheek covered by three plates, including a large submarginal.

Apomorphies acquired at the following numbered stages are: 2, premedian plate, and backward shifting of the nasal capsules, with nostrils opening at the level of, or just in front of, the orbits; 3, tesserae on the skull roof, particularly in the pineal and orbital regions; 4 (rhenanid apomorphies), pseudobatoid body shape with very flattened skull, loss of the dermal cervical joint, fragmented (or tessellated) anterolateral and spinal plates, strong reduction in body armour length, and loss of the posterior dorsolateral and posterolateral plates; 5, large premedian plate with a preorbital depression, dermal cervical joint with a fossa on the articular flange of the anterior dorsolateral plate, external endolymphatic pore placed medially relative to the endocranial opening, and strong cohesion of the plates covering the endoskeletal shoulder girdle to form a pectoral unit (anterolateral, spinal, anterior ventrolateral plates); 6 (antiarchan apomorphies), a second (posterior) median dorsal plate incorporated in the body armour, pectoral unit represented by a single plate (anterior ventrolateral) enclosing the small pectoral fenestra, pectoral fin modified into a slender appendage covered by plates derived from modified scales, antiarch skull roof pattern with the orbits laterally enclosed by large lateral plates, and semilunar plates present; 7, dermal bone ornamented with evenly distributed tubercles of pallial semidentine; 8, anterior and posterior median ventral plates added to the body armour, and endolymphatic duct opening on the same paranuchal plate as the confluence of the posterior pit-line and the main lateral line of the skull; 9, sensory lines enclosed in tubes projecting below the visceral surface of the dermal skull plates and opening by pores, central sensory line lost, X pattern of the sensory lines on the middle plate of the skull (nuchal or post-pineo-nuchal), fragmentation of the suborbital and post-suborbital plates, and similar structure of the cervical joint; 10 (ptyctodontid apomorphies), loss of rostral plate, endolymphatic duct closed, loss of suborbital and post-suborbital plates, loss of posterior dorsolateral, posterolateral, posterior ventrolateral, posterior median ventral, presence of bony pelvic claspers; 11 (petalichthyid apomorphies), laterodorsal orbits, bounded laterally by pre- and post-orbital plates and medially by the central plate; 12, shortened preorbital region of the skull, and separate interolateral plate with a deep transverse ventral groove; 13 (phyllolepid apomorphies), flattened body, much expanded nuchal plate, loss of rostral plate, loss of posterior dorsolateral and posterolateral plates, and loss of semidentine on the superficial ornament; 14 (arthrodire apomorphies), two pairs of upper tooth plates, large endocranial posterior postorbital processes, wide and short rostral plate, and pectoral fenestra closed posteriorly by the posterolateral and the posterior ventrolateral plates unless secondarily transformed into a deep pectoral emargination in some brachythoracids.

ventral in various antiarch genera (it may even be replaced by several platelets), I regard this plate as an anamestic component of the antiarch body armour, filling the space between the anterior and posterior ventrolateral plates, and arising independently of the posterior median ventral in arthrodires.

The other homologous plates of the body armour in antiarchs and arthrodires were already present in the common ancestor of placoderms, and posterior elongation and/or enlargement of pre-existing elements are the only processes required to obtain the box-like armour. There is then no contradiction in considering the long body armour in both groups as convergently acquired. The differences in its composition in both groups support this view.

The assumed closer relationships between the dolichothoracid arthrodires and antiarchs has certainly been influenced by the ideas developed by Westoll (1945) and retained by Denison (1978: 10) concerning the derivation of the pectoral appendage in antiarchs from a long spinal plate similar to that of the Dolichothoraci. However the discovery of a distinct spinal process in the Yunnanolepiformes (Zhang, 1978), together with a pectoral derivation of this appendage from a spinal plate. On the contrary, it confirms its nature as a modified fin. In any case, as a modified spinal, one may ask why its origin was sought among the Dolichothoraci, since the petalichthyids also have long and stout spinals. Presumably, the reason was the general similarity of the box-like body armour in arthrodires and antiarchs.

The new phylogenetic scheme presented here implies also the following convergences in the evolution of the body armour: the posterior dorsolateral plate has been lost independently in rhenanids, ptyctodontids, and phyllolepids, and the same applies to the posterolateral plate in rhenanids and the common ancestor of ptyctodontids and petalichthyids.

My last remark on the body armour is to stress that its initial composition — as deduced from the matrix of Fig. 6 — is identical to that of the Acanthothoraci, insofar as this is currently known. In addition, the other apomorphic characters of the proposed scheme, and the groupings they lead to, require a partition of the Acanthothoraci, which was initially considered a monophyletic group on the basis of one uniquely-derived character: the shape of the occipital margin of the skull with posteriorly-projecting paranuchals. By retaining the monophyly of the Acanthothoraci, the apomorphies and assumed monophyly of some of the best-founded groups of placoderms (e.g. the antiarchs) would have to be dismissed. Either the initially accepted monophyly of the Acanthothoraci, or the monophyly of all the other groups, must be rejected, and I have chosen the first alternative. I suggest that the Acanthothoraci play in the phylogeny the role of a stem-group, its members being scattered as sister-groups of several major placoderm orders. This solution was earlier proposed by Obruchev (1964, 1967), but in the present case is not put forward by reason of their geological antiquity (which has since been proven false; Westoll, 1967), but strictly on the distribution of homologous characters shared with other placoderms. Nevertheless the Acanthothoraci can still be distinguished by their general morphology from the other placoderms, as is often the case with paraphyletic groups.

One evident weakness in the proposed cladogram is the position of *Radotina prima*. This form has terminal nasal capsules and a well developed 'rostrum', but neither a premedian plate nor tesserae. In brief, it exhibits only (assumed) primitive characters. However, its dermal bone bears closely set tubercles, apparently non-stellate, even if this detail is not mentioned by Gross (1958: 21). This taxon could be placed in a multiple branching of the base of the cladogram (if the available information on its morphology were considered insufficient), but the position proposed in Fig. 12 is based on the assumption that the ornament of *Radotina prima* is made of pallial semidentine, a detail which remains to be confirmed. This position in the cladogram raises the taxonomic question of membership in the genus *Radotina*. The available data on all other species of the genus indicate that *R. prima* does not belong here, and until the type material is redescribed I propose to mention *'R. prima'* between quotation marks as in the present cladogram.

Other weaknesses in this new scheme follow mainly from the absence of adequate outgroup comparison at the proper level to test the phylogenetic significance of some of the basic characters of placoderms (e.g. the initial state of the dermal skeleton). However the scheme forms a basis for future research, when precise tests can be worked out to attempt to falsify the interrelationships proposed. I guess the best tests will come from studies of the 'Acanthothoraci', a group of central importance for our problem. I am confident that some of the keys to understanding placoderm phylogeny will come from investigations of this group.

My final remark is to stress the difficulties in building a practical classification from a cladogram which includes a stem-group, as is the case in the present example. We meet the same problems as encountered when classifying fossils with extant groups: the terminal taxa rule the system. However I see no real objection to abandoning the group 'Acanthothoraci' in a formal cladistic classification, should further studies confirm it as a non-monophyletic group. It can then be retained for its practical use as a vernacular term.

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LIST OF ABBREVIATIONS

ADL — anterior dorsolateral plate
ADL oa — overlap area for the anterior dorsolateral plate
AL — anterolateral plate
AMD — anterior median dorsal plate
AMV — anterior median ventral plate
art 1 — articular lamina of the paranuchal plate
C — central plate
Ca — anterior central plate
Cp — posterior central plate
cc — central sensory line
d end — external foramen for the endolymphatic duct
IL — interolateral plate
L — lateral plate
lc — main lateral line of the head
M — marginal plate
MD — median dorsal plate
mp — middle pit-line of the skull
MV — median ventral plate
MxL — mixilateral plate
N — nuchal plate
no — anterior nostril
occ — occipital sensory line
PaN — paranuchal plate
PaNa — anterior paranuchal plate
PaNp — posterior paranuchal plate
PDL — posterior dorsolateral plate
PDL oa — overlap area for the posterior dorsolateral plate
pelv — pelvic dermal plate
pf — pectoral fenestra
Pi — pineal plate
pi — pineal pit
PL — posterolateral plate
PL oa — overlapping area for the posterolateral plate
pmc — postmarginal sensory line
PMD — posterior median dorsal plate
PMV — posterior median ventral plate
PN — post-nasal plate
po — pores of the sensory tubes
Pp — post-pineal plate
pp — posterior pit-line
PrO — preorbital plate
Prm — premedian plate
PSO — post-suborbital plate
PtO — postorbital plate
PVL — posterior ventrolateral plate

PVL oa — overlapping area for the posterior ventrolateral plate
ScCo — endoskeletal shoulder girdle
SL — semilunar plate
SM — submarginal plate
SO — suborbital plate
soc — supra orbital sensory line
Sp — spinal plate
R — rostral plate.